Original article

Word count = 9367

Survival histories of marsupial carnivores on Australian continental shelf islands highlight climate change and Europeans as likely extirpation factors: implications for island predator restoration

David E. Peacock [1*], Bronwyn A. Fancourt [2,3], Matthew C. McDowell [2,4] and Ian Abbott [5]

[1] Biosecurity SA, Adelaide SA 5001, Australia.

[2] School of Biological Sciences, University of Tasmania, Hobart TAS 7001, Australia

[3] Present address: Pest Animal Research Centre, Biosecurity Queensland, Department of Agriculture and Fisheries, Toowoomba QLD 4350, Australia

[4] School of Biological Sciences, Flinders University of South Australia, Adelaide SA 5001, Australia.

[5] 1 Caddy Avenue, West Leederville WA 6007, Australia.

* Correspondence: David E. Peacock, Biosecurity SA, GPO Box 1671, Adelaide, Australia.

E-mail: david.peacock@sa.gov.au

Running head: Marsupial carnivore survival on Australian continental shelf islands

Abstract

Aim

To examine the survival histories and potential extirpation factors of five large marsupial carnivores that once occurred on three large Australian continental shelf islands to inform predator restoration efforts to Kangaroo Island.

Location

Kangaroo Island, King Island and Flinders Island - located on the continental shelf off the southern coastline of the Australian mainland.

Methods

A review of historical accounts and fossil evidence. Primary source of marsupial carnivore records was the National Library of Australia's online newspaper digitisation website, Trove, covering the period 1803–1954. Additional sources included books and diaries written by explorers, visitors or early settlers; relevant natural history, agriculture and science journals and zoological books; and fossil specimens and museum records of marsupial carnivores.

Results

The pattern of species persistence and extirpation on Kangaroo Island parallels those observed on King and Flinders Islands. Fossil data supports the terminal Pleistocene–early Holocene extinction of the thylacine (*Thylacinus cynocephalus*) from Kangaroo Island and the Tasmanian devil (*Sarcophilus harrisii*) from both Kangaroo and Flinders Islands. Though eastern quoll (*Dasyurus viverrinus*) fossils have been found on Kangaroo and Flinders Islands, and *D. geoffroii* on Kangaroo Island, contemporary evidence for their post-European persistence is unclear. In contrast, fossil, museum and anecdotal data supports the presence of the spotted-tailed quoll (*Dasyurus maculatus*) on all three islands and, contrary to established knowledge, its post-European persistence on Kangaroo Island.

Main Conclusions

The loss of *T. cynocephalus*, *S. harrisii*, *D. geoffroii* and *D. viverrinus* appear to be commensurate with late to terminal Pleistocene–early Holocene climate change and associated changes in vegetation communities. In contrast, anthropogenic persecution of *D. maculatus* appears to be the principal cause of its post-European extirpation. We recommend *D. maculatus* as a suitable candidate marsupial carnivore for reintroduction to Kangaroo Island, and possibly King and Flinders Islands.

Keywords

Dasyurus maculatus, Dasyurus viverrinus, extinction, Flinders Island, Kangaroo Island, King Island, marsupial carnivore, persecution, persistence, *Sarcophilus harrisii*

Introduction

The world has suffered exceedingly rapid biodiversity loss over recent centuries (Stuart *et al.*, 2004; Pimm *et al.*, 2006; Hoffmann *et al.*, 2011). A pervasive suite of processes including habitat loss, introduced species and pathogens, overexploitation, persecution and anthropogenic climate change have all expedited the rapid loss of species at rates up to 100 times faster than the background rate of extinction (Brook *et al.*, 2008; Ceballos *et al.*, 2015). As multiple species are lost from each trophic guild, key ecosystem functions are also lost, resulting in ecosystem instability and erosion of their resilience to interminable global change. To conserve biological diversity, conservation efforts need to focus on restoring the most depauperate guilds in order to reinstate missing ecosystem function and resilience (Walker, 1995).

Predators perform an important ecological function through the density and behavioural mediation of smaller predators and prey species (Palomares & Caro, 1999; Creel &

Christianson, 2008; Suraci *et al.*, 2016). Accordingly, the loss of predators may trigger trophic cascades that can disrupt ecosystem structure and processes, potentially threatening a range of animal and plant species (Crooks & Soulé, 1999; Estes *et al.*, 2011; Bertness *et al.*, 2014). But many of the world's predators are in a parlous state, suffering marked declines in both abundance and range (Ripple *et al.*, 2014). Often persecuted for habitat loss driven conflicts with humans and livestock (Woodroffe *et al.*, 2005). Many large carnivores are listed as threatened with extinction and continue to suffer ongoing population declines (Ripple *et al.*, 2014).

In Australia, native predators have been lost from vast areas of the landscape, leaving many ecosystems dominated by introduced predators such as the dingo (*Canis lupus dingo*) and wild dog (*C. l. familiaris*) hybrids, European red fox (*Vulpes vulpes*) and feral cat (*Felis catus*) (Woinarski *et al.*, 2015). All members of Australia's native marsupial carnivore guild are either extinct or currently threatened with extinction within greatly reduced ranges. The last known thylacine (*Thylacinus cynocephalus*; 15-35 kg) died in captivity in 1936 (Guiler, 1985). The Tasmanian devil (*Sarcophilus harrisii*; 5-12 kg) and eastern quoll (*Dasyurus viverrinus*; 0.7-2.0 kg) are both endangered and now survive only on the island of Tasmania where both species have suffered marked population declines over the past 15-20 years (Hawkins *et al.*, 2006; Fancourt *et al.*, 2013). The endangered northern quoll (*D. hallucatus*; 0.25-1.1 kg) has suffered severe population decline and localised extinctions across northern Australia (Woinarski *et al.*, 2011), while the western quoll (*D. geoffroii*; 0.6-2.1 kg) is currently considered conservation dependent (Woinarski *et al.*, 2014). The larger spotted-tailed quoll (*D. maculatus*; 0.8-5.0 kg) is restricted to eastern Australia, including Tasmania, and is considered endangered (mainland population) or vulnerable (Tasmanian population) throughout its range (Woinarski *et al.*, 2014). Since their introduction following European settlement just over 200 years ago, cats and foxes have decimated populations of medium and small sized native animals across much of the continent (Burbidge & McKenzie, 1989; Woinarski *et al.*, 2015). Several of Australia's offshore islands form natural conservation refuges that enable a range of threatened species to persist in the absence of introduced predators and competitors (Burbidge, 1999), while others have been established following eradication of introduced predators (Morris *et al.*, 2015).

One issue often faced by conservationists in restoring ecosystem resilience is a lack of, and hence erroneous, knowledge of the species that historically persisted in areas of conservation interest or concern. For example, while the eastern and western quolls were formerly very common and widespread, only limited museum samples exist to establish their former distributions. Additionally, shifting baselines and intergenerational amnesia can result in primary components being lost from modern knowledge (McDowell, 2014; Alleway & Connell, 2015). Historical accounts and sub-fossil specimens are increasingly critical components of modern efforts at re-establishing species former distributions, and hence the associated ecosystems.

Kangaroo Island, Australia's third largest island (4 405 km^2), is located approximately 13 km off the Australian mainland, 110 km south-west of Adelaide (Fig. 1). It has a Mediterranean climate (Schwerdtfeger, 2002), with mean annual rainfall ranging from 489 mm at Kingscote in the east to 625.9 mm at Cape Borda in the west (www.bom.gov.au). While 51% of the island's vegetation has been cleared since 1836, predominantly for agriculture (Robinson & Armstrong, 1999), remnant native vegetation covers approximately 47% of the island, with around two-thirds of this conserved within reserves or heritage agreements (Ball & Carruthers, 1999) (Fig. 1). The island retains a relatively intact diverse native fauna, primarily due to the absence of introduced European rabbits (*Oryctolagus cuniculus*) and foxes. However, the island does face a number of management issues, including introduced feral cats and Indian peafowl (*Pavo cristatus*), as well as high abundance of several native species including the common brushtail possum (*Trichosurus vulpecula*), tammar wallaby (*Macropus eugenii*), western grey kangaroo (*M. fuliginosus*) and the introduced koala (*Phascolarctos cinereus*). These high native abundances have likely been facilitated by clearance of native vegetation, establishment of introduced pastures (Robinson & Kemper, 1999) and the modern-day absence of a large native predator. It is possible that the reintroduction of a native predator to Kangaroo Island could achieve multiple conservation benefits by contributing to the conservation of a threatened marsupial carnivore while restoring crucial ecosystem function that could contribute to the conservation of other threatened species. However, very little is known about the former native predator guild on Kangaroo Island, when these species went locally extinct, or the reasons for their extirpation. Such information is crucial to inform reintroductions, as success will ultimately depend on ensuring the appropriate species is reintroduced, and that the threatening processes that drove the species to local extinction have been removed or adequately ameliorated.

The comparison of historic faunal assemblages recorded on similar islands and the likely reasons for their extirpation may help in understanding the fate of the former predator guild on Kangaroo Island. King Island and Flinders Island are located within Bass Strait off the southern coast of mainland Australia, approximately midway between Tasmania and the mainland (Fig. 2). Both islands have a temperate maritime climate, and like Kangaroo Island, were connected with the Australian mainland by a continental land bridge during global glacial phases (ice ages) when sea-levels were around 125 m lower than current levels (Fig. 2). However, during global warm phases (interglacial), the islands become isolated from mainland Australia by elevated sea-levels (Fig. 2). The Holocene transgression resulted in rapid global sea-level rise that isolated Kangaroo Island from the Australian mainland at about 8.9 kya, reaching present sea level at 7.5 kya (Belperio & Flint, 1999). Similarly, King

Island and Flinders Island became isolated around 11 kya and 10 kya respectively (Jennings, 1971).

While both King Island (1 098 km^2; mean rainfall 856 mm) and Flinders Island (1 367 km^2; mean rainfall 737 mm) are smaller than Kangaroo Island, their connectedness through the continental land bridge and similar southern latitudes suggests that their historic remnant faunal assemblages may have shared many similarities with Kangaroo Island. Accordingly, combined evidence from these three islands may be used to inform which native predators formerly persisted on Kangaroo Island and the possible reasons for their extirpation. Such fundamental knowledge is important for understanding whether native predators could realistically be reintroduced to Kangaroo Island, and if so, which species would be most suitable under current conditions.

In this study, we review and evaluate contemporary, historic and fossil evidence of native predators on Kangaroo Island in order to understand which species formerly occurred there, time since extirpation, and the likely causes for their local extirpation. We then compare contemporary, historic and fossil evidence of predator guilds on King and Flinders Island to understand the persistence of these species on islands that were similarly isolated from the Australian mainland around the same time as Kangaroo Island. After reviewing all of the available evidence, we recommend which native predator would likely be the most suitable species for reintroduction to Kangaroo Island, and discuss potential benefits and challenges associated with such a reintroduction.

Figures 1 and 2 here

Methods

Numerous sources were searched for this study, as detailed in Peacock and Abbott (2013). The National Library of Australia's online newspaper digitisation website, Trove, was searched for 1803–1954 (with coverage of some to 1981). Primary search terms were the contemporary names "native cat" and "tiger cat", with "tiger cat" assumed to refer to *D. maculatus*. "Native cat" is however less definitive; many early settlers and naturalists often used "native cat" to refer to *D. viverrinus and*/or *D. geoffroii.* However it was also used more generally to distinguish between "native" cats and "domestic cats gone wild", and hence "native cat" can occasionally refer to any of the quoll species and is therefore not necessarily diagnostic of *D. viverrinus*/*D. geoffroii*. Furthermore, some species observations may be misidentified, as still commonly occurs today with *D. viverrinus* and *D. maculatus* often being confused. For this review, we have assumed 'native cat' primarily refers to *D. viverrinus* while acknowledging this may be uncertain. In total 19,500 accounts were reviewed from 620 newspapers, with >3100 accounts considered informative about quolls in Australia. Additional sources included books and diaries written by visitors or early settlers; reports of parliamentary debates, select committees, royal commissions, boards of inquiry, annual reports of government departments, acts of parliament, and government gazettes; relevant natural history, agriculture and science journals and zoological books.

We also reviewed fossil and museum specimens and records of marsupial carnivores listed on the Atlas of Living Australia, the Tasmanian Natural Values Atlas and the Online Zoological Collections of Australian Museums. To minimise the likelihood of duplicate records, museum records were cross-referenced to literature or historic accounts wherever possible. We acknowledge that several accounts may refer to a single observation or event, however in the absence of complete information, any such duplication is unavoidable.

For each of the three islands, records were summarised in a table (see Appendix S1 to S3 in Supporting Information) listing evidence and accounts considered informative for estimating the presence or absence of *D. viverrinus*, *D. geoffroii*, *D. maculatus*, *S. harrisii* and *T. cynocephalus*. Additionally, two tables were developed (see Appendix S4 for Kangaroo Island and S5 for Flinders and King Islands) listing accounts or observations considered informative as to the likely factors that may have contributed to each species' extirpation. For the convenience of readers, some accounts are duplicated, either fully or partially, in both tables for each island, wherever the account was informative to both questions.

Results

Occurrence and persistence

The contemporary and fossil evidence for the presence of each marsupial carnivore on each island is detailed below and summarised in Table 1.

Insert Table 1

Kangaroo Island

While fossil evidence indicates that five marsupial carnivore species occurred on Kangaroo Island (Table 1), it appears that only *D. maculatus* persisted until European settlement. Walshe (2014; see Appendix S1) radiocarbon dated a *D. maculatus* dentary collected from a European archaeological assemblage to 1730-1800 AD, confirming the species remained extant on Kangaroo Island when the earliest Europeans arrived. Observations recorded by the French explorer Péron suggest the species was still extant in 1802 (Lesueur & Petit, 1807; Péron & de Freycinet, 1816), and Leigh (1839) recorded an observation that suggests the species was still being encountered on Kangaroo Island in 1837 (Appendix S1). Whilst far from diagnostic, the description by Leigh (1839) identifies characteristics such as size *"…a large wild-cat, half as large again as the domestic one…*" and colouration *"…and was spotted upon a brown ground with raw umber…*" that are more comparable to *D. maculatus* than to *D. viverrinus* or *D. geoffroii*. In contrast, Waite and Wood Jones (1927) state that *D. viverrinus* "*…is apparently the only carnivorous marsupial that existed on the island…*", however this statement was based on accounts relayed from some older inhabitants of the island rather than direct observation. They also state that "*Some of the older inhabitants remember having seen a few individuals many years ago, and a single mandible was found in a bone hole at Cape de Couedic, during the visit of the Board in November, 1923*...".

However, this specimen could not be located, nor its age confirmed. *Dasyurus viverrinus* occurs in the fossil record from Kelly Hill Cave as recently as 2.5-1.7 kya (McDowell, 2013; Adams *et al.*, 2016). *Dasyurus geoffroii* and *Thylacinus cynocephalus* specimens have been recovered from the same assemblage, but are much older (17.7-13.6 and 15.5-13.1 cal. kya respectively; Appendix S1; McDowell unpublished data) than the other dasyurids and apparently disappeared from the region before Kangaroo Island was isolated by Holocene rising sea-levels.

There are no contemporary records of *D. viverrinus* or *D. geoffroii* from Kangaroo Island. As Waite and Wood Jones (1927) were clearly unaware of the modern presence of *D. maculatus* (that has been subsequently confirmed by Walshe 2014) , it is possible that the species may have been confused and that the inhabitants were in fact referring to *D. maculatus*. With the possible exception of an undated *S. harrisii* tooth fragment collected from the floor surface of Kelly Hill Cave, there is no evidence that *S. harrisii* persisted beyond 6.9-6.3 kya (Langeluddecke, 2001) shortly after Kangaroo Island was isolated by rising sea-levels, with *T. cynocephalus* last evident at 12.4–13.2 kya (McDowell *et al.*, 2015).

King Island

As noted for Kangaroo Island, the only modern-day evidence of marsupial carnivore species persisting on King Island was for *D. maculatus* (Table 1 and Appendix S1), with the last confirmed specimen collected in 1922 (Museum Victoria skin: R8235). Using bones collected from sand blows on King Island, Spencer and Kershaw (1910) described *D. bowlingi* as a new species distinct from *D. maculatus*, stating "*…we are of opinion – first, that the Dasyurus remains include those of two species; secondly, that the larger of these two* [D. bowlingi] *is distinct from any yet described; and, thirdly, that the smaller form is identical with D. maculatus.*" However, after re-examining the specimens, Marshall and

Hope (1973) later interpreted *D. bowlingi* as the larger morph (male) of the sexually dimorphic *D. maculatus*.

When referring to species collected from King Island in 1802, Péron and de Freycinet (1816) state that they collected "*deux Dasyures élégans* [two Dasyures elegans]". However, it is not clear whether they collected two different species of Dasyure, or two individuals of a single Dasyure species. A margin note adjacent to the text refers to "Plate XXXIII" in the accompanying atlas (Lesueur & Petit, 1807), on which two *D. maculatus* are drawn, suggesting that they may have collected two individuals of *D. maculatus*. However, as noted by Marshall and Hope (1973): p. 226, "*…one cannot place too much confidence in the juxtaposition of Plate XXXIII with the text, as Péron died in 1910* [1810], *halfway through the compilation of Vol II, which was completed by de Freycinet.*" Accordingly, the only link between the text and the image of *D. maculatus* was made after Péron's death. It is also possible that the two Dasyures were actually *D. maculatus* and *D. viverrinus*, although this cannot be confirmed. Lesueur and Petit's (1807) atlas does not include any illustration of *D. viverrinus*, however several species were listed as being collected for which there is no corresponding illustration in the atlas. While there is no evidence of modern-day *D. viverrinus* occurring on King Island, there are two references to "native cats" (1866 and 1906) that may have referred to either *D. viverrinus* or *D. maculatus*, however a reliable identification cannot be resolved from either of these accounts (see Appendix S2). As mentioned previously, the variable use of the term "native cat" contributes to the ambiguity of these accounts. Both *D. viverrinus* and *D. maculatus* are often confused in Tasmania today, suggesting that anecdotal observations or reports are typically less reliable for species identification than physical evidence. The absence of any fossil or sub-fossil evidence of *D. viverrinus* suggests that these observations likely refer to *D. maculatus*. This is further supported by several accounts that specifically noted the absence of *D. viverrinus* on King

Island (see Appendix S2). It should be noted that while there is no fossil or sub-fossil evidence of *T. cynocephalus*, *S. harrisii* or *D. viverrinus* on King Island (Table 1), this may simply reflect the absence of a datable stratigraphic deposit on the island similar to the caves and deposits excavated on Kangaroo Island.

Flinders Island

There is no contemporary evidence of marsupial carnivore persistence on Flinders Island, however both “native cats” and “tiger cats” were reported on the island between 1835 and 1928 (see Appendix S3), suggesting that either *D. maculatus* and/or *D. viverrinus* persisted until after European settlement on the island. While there are no records of *T. cynocephalus* on Flinders Island, *S. harrisii* and *D. maculatus* are recorded from postglacial sand blows at Palana, and *D. viverrinus* is represented in Ranga Cave from c. 8.2 kya (Hope, 1974; see Appendix S3).

Causes of extirpation

Hope *et al.* (1977) propose possible reasons for the changes in the late Pleistocene and early Holocene mammal, bird and reptile fauna on Kangaroo Island in relation to the Seton rock shelter deposit (see Appendix S4). However, McDowell *et al.* (2015) demonstrated that faunal change in the Seton rock shelter assemblage was probably caused by a change in collection agent. However, this does not invalidate Hope *et al*.’s argument. Additional prehistoric and contemporary accounts and insights for Kangaroo Island are listed in Appendix S4, and for King and Flinders Islands in Appendix S5.

Prehistoric factors

The disappearance of many non-volant mammals from the fossil record commenced around 12-7 kya, including *S. harrisii* and later *D. viverrinus* coinciding with rapid Holocene climate change that caused sea levels to rise and inundate continental land-bridges, isolating Australia's land-bridge islands (Hope *et al.*, 1977; Lambeck & Chappell, 2001; Adams *et al.*, 2016, Fig 7). Recent climatic modelling and reconstruction by Saltre *et al.* (2016) indicates that the velocity of climate change was more pronounced around 12-7 kya than at any other time in the preceding 100 kyr, with marked increases in temperature and precipitation. The shift from a cool, dry climate to warm, wet conditions would have rendered the newly isolated Kangaroo, King and Flinders Islands unsuitable for many species. Pollen records from Kangaroo Island lake cores suggest the late Pleistocene was characterised by more open grasslands that were subsequently replaced with more dense heath-woodland and forests during the Holocene (Clark & Lampert, 1981; Singh *et al.*, 1981). This is reflected in the fossil fauna (Hope *et al.*, 1977; Adams *et al.*, 2016) and the thick vegetation observed by early European explorers on all three islands in c. 1800 (Appendix S4 and S5). This is further supported by stable isotope analyses of modern and fossil *Macropus* spp. tooth enamel from Black Creek Swamp, Kangaroo Island, which indicated a shift in diet and environmental conditions from C4-inclusive mixed habitats (woods and open grasslands) during the late Pleistocene, to C3-only wooded and closed canopy habitats today (Forbes *et al.*, 2010). This shift is consistent with charcoal records (Clark & Lampert, 1981; Singh *et al.*, 1981) that indicate reduced fire frequency that may indicate the disappearance of indigenous humans around 4–2.5 kya (Taylor, 2002 citing Jones 1977). The loss of many cool-adapted species from the fossil record (Hope *et al.*, 1977) is also consistent with the warming temperatures of the early Holocene, with many of these species now only found in Tasmania and parts of south-eastern Australia. The insular nature of the islands would have prevented non-volant mammals from escaping to more suitable habitat, possibly contributing to their extirpation around that time.

Contemporary factors

Kangaroo Island was believed to be uninhabited in the early 1800s when European explorers first landed on the island (Péron & de Freycinet, 1816; Hope *et al.*, 1977; Draper, 1999). However, a few years later and until formal settlement in 1836, over 500 sealers frequented the island (Robinson, 1999). Leigh (1839) reports shooting at what appears to be a *D. maculatus* for attacking domestic poultry in 1837, and "at length" shooting one. *Dasyurus maculatus* was the second most numerous species recovered from a European archaeological skinning site at Bales Bay (Walshe, 2014). Regardless of the reason they were killed, this suggests the species was persecuted by early European inhabitants of Kangaroo Island. As the native vegetation was thick during the early years of settlement (Leigh, 1839; Draper, 1999) and, contrary to Hope *et al.* (1977), still c. 80-85% intact in 1945 (see Fig. 2.4; Interdepartmental Committee on Vegetation Clearance, 1976), this strongly suggests habitat loss was not the primary factor causing the extirpation of *D. maculatus*.

Sealers and fishermen arrived on King Island in the early 1800s, although their presence was short-lived and the island remained deserted for many years (Appendix S5; Spencer & Kershaw, 1910; Threatened Species Section, 2012). Flinders Island was temporarily used as a mission for the Tasmanian Aboriginals in the 1830s (Plomley, 1966, 1987), but like King Island, it was not inhabited to any great extent until the end of the 19th century (Hope, 1973). During this time, many feral dogs persisted on the Bass Strait islands, possibly left there by the sealers (see Appendix S5), and may have depredated *D. maculatus* and/or *D. viverrinus*. On King Island, the last confirmed *D. maculatus* was taken in 1922 (see Appendix S2) and sightings were reported as recently as the 1950s (Threatened Species Section, 2012). By this time, much of the suitable habitat had been cleared for settlement and agriculture, and the species had been persecuted for taking domestic poultry and supplies (see Appendix S2), with these factors likely contributing to the species' demise on the island. On Flinders Island, the last reported sighting of *D. maculatus* was 1893, with reports of *D. viverrinus* being seen in 1928 (see Appendix S5). While no contemporary evidence has been found to support these reports, the combination of persecution together with habitat loss for settlement and agriculture mirrors that reported from King Island (see Appendix S5), suggesting these factors would also likely have contributed to the extirpation of these species by that time.

Discussion

Fossil evidence indicates that *T. cynocephalus, S. harrisii, D. maculatus, D. geoffroii* and *D. viverrinus* all occurred on Kangaroo Island during the late Pleistocene (prior to islandification) and/or early Holocene. However, contemporary and fossil evidence both suggest that only *D. maculatus* persisted until the early days of European settlement. Fossils of *D. maculatus* occur in the uppermost layer of Kelly Hill Cave dated 0.32–0.0 kya (McDowell unpub. data), a dentary from Bales Bay has been directly radiocarbon dated to 1730–1800 AD (Walshe, 2014) and a possible sighting and shot animal was reported from Kangaroo Island in 1837 (Leigh, 1839). The absence of any further reports suggests that the species became locally extinct soon after, with persecution the probable primary cause. However, its extinction from largely intact habitat raises the possibility that other factors such as disease, as for example seen in frogs (Berger *et al.*, 1998), bats (Blehert *et al.*, 2009) and Tasmanian devils (McCallum *et al.*, 2009). The quoll disease accounts and hypothesis in Peacock and Abbott (2014) may also have been a primary factor. Whilst we acknowledge that absence of evidence does not confer evidence of absence, the patterns of species persistence and extirpation parallels those observed on King and Flinders Islands. Accordingly, as *D. maculatus* is now legally protected from persecution, and as extensive suitable habitat still exists, we recommend that *D. maculatus* would be the preferred candidate marsupial carnivore for reintroduction to Kangaroo Island.

Our findings of marsupial carnivore persistence on continental shelf islands differ, in part, to the biogeographical analyses and conclusions of Lavery *et al.* (2013). By comparing pre-colonisation species persistence to fauna of the adjacent zoogeographic province, Lavery *et al.* (2013) concluded that overall, dasyurids are less likely to persist on continental shelf islands than other taxa. However, Lavery *et al.* (2013) also reported that islands in the south-west semi-arid and Bassian provinces did not conform to their general findings. This is consistent with our findings that a large marsupial carnivore persisted on (Bassian) King Island (and possibly Flinders Island). However, as evidence for the post-colonisation persistence of *D. maculatus* on Kangaroo Island is presented here for the first time, Lavery *et al.* (2013) may have inadvertently excluded it from pre-colonisation species distributions used in their modelling, contributing to their different conclusions for the south-east semi-arid province. Furthermore, Lavery *et al.* (2013) state that the carnivorous diet and large home range requirements of dasyuromorphs make them less likely to persist on small islands. However, these factors would be less limiting on an island as large as Kangaroo Island, particularly for *D. maculatus* which is well-adapted to exploit both terrestrial and arboreal niches.

While *T. cynocephalus* apparently last occurred in the Kangaroo Island fossil record 15.5-13.1 kya, prior to islandification, evidence suggests *S. harrisii* and *D. viverrinus* persisted until around 6.9-6.3 kya and 2.5-1.7 kya respectively (Appendix S1). Their subsequent disappearance from the fossil record formed part of a significant change in species richness and composition, from open habitat species to forest dwelling species (Hope *et al.*, 1977). These changes are well documented for the adjacent Australian mainland and were attributed by Hope *et al.* (1977) to a reduction in open vegetation probably due to a rapidly changing climate, transitioning from the cooler, drier terminal Pleistocene to the warmer, wetter Holocene (Singh *et al*., 1981; Forbes 2010; Adams *et al*., 2016). Indeed, recent climatic modelling and reconstruction by Saltre *et al.* (2016) indicates that the velocity of climate change was more pronounced around 12-7 kya than at any other time in the preceding 100 kyr, with marked increases in temperature and precipitation. Additionally, carbon isotope analysis by Forbes *et al.* (2010) revealed a shift in diet and environmental conditions from woodlands and open grasslands during the late Pleistocene to only wooded and closed canopy habitats today, further supporting this hypothesis. However, the change in guild structure observed by Hope *et al.* (1977) in the Seton rock shelter deposit also coincided with an increased abundance of stone tools in the accumulation, suggesting that apparent changes in species richness and faunal composition possibly related to a change in collection agent rather than climate. A recent study by McDowell *et al.* (2015) further supports this explanation, suggesting that units aged 21-17 kya were primarily accumulated by *S. harrisii* and owls, after which humans became the primary accumulation agent. While a change in accumulation agent is likely true, these two alternative explanations are not necessarily mutually exclusive. Rapid global warming following the Last Glacial Maximum caused rapid sea level rise, flooding the continental land bridge that connected Kangaroo Island to the Australian mainland. The reduction in land area would have increased hunting pressure and inter- and intra-specific competition on the island, whilst the increasing vegetation density triggered by the warmer, wetter conditions would have rendered the island unsuitable for many open habitat specialists, further reducing species abundance. These changes would have been further facilitated by fire frequency reduction attributed to the disappearance of humans from the island about 4 kyr ago, resulting in the thick, closed vegetation evident in accounts from early European explorers and settlers on Kangaroo Island (see Appendix S4).

The patterns of persistence and extirpation of marsupial carnivores on Kangaroo Island are comparable to those of King and Flinders Islands. While *S. harrisii*, *D. maculatus* and *D. viverrinus* all occur in the fossil records of Ranga Cave and/or the Palana sand blows on Flinders Island (see Appendix S3), there is no contemporary evidence that any of these species persisted on the island until European settlement. However, anecdotal reports suggest that either *D. maculatus* and/or *D. viverrinus* persisted until the early 1920s (Table 1). The paucity of fossil evidence on King Island (Table 1) may simply reflect survey bias, as the island lacks any deposits similar to those containing the remains of late Pleistocene and early Holocene marsupial carnivores on Kangaroo and Flinders Island (Hope, 1973). However, contemporary evidence including skulls and skins of *D. maculatus* collected from King Island as recently as the early 1920s demonstrates that the species was present, and persisted to coexist with Europeans in the early days of settlement (see Appendix S2). Between the time the Bass Strait islands finally took shape at about 8 kya and the arrival of European explorers at the end of the 18th century, several species including *S. harrisii* and possibly *D. viverrinus* disappeared completely from the Bass Strait islands (Hope, 1973). As noted for Kangaroo Island, many of these species were probably negatively affected by the reduction or disappearance of suitable habitat on the islands, due either to a reduction in size of the islands, climatic change or a combination of both factors. The absence of human activity for several thousand years prior to the arrival of sealers and European settlers would have reduced fire frequency which, combined with increasing temperatures and precipitation, would likely have caused a shift in vegetation cover that rendered the islands unsuitable for many species of open habitats. This hypothesis is further supported by the dense vegetation observed in the early accounts of European explorers (see Appendix S5).

Commented [1]: Do we need change this to bring into line with changes made earlier in the paper?

The shift in climate and associated vegetation changes would have likely rendered Kangaroo Island less suitable for *D. viverrinus, D. geoffroii* and *S. harrisii* whilst improving the suitability for *D. maculatus*. Recent weather modelling by Fancourt *et al.* (2015) suggests that *D. viverrinus* is more strongly associated with cool, dry conditions, similar to those experienced on Kangaroo Island in the late Pleistocene, whereas the warm, wetter conditions of the early Holocene would have been less suitable for the species' persistence. The associated shift from more open vegetation to dense scrub and closed canopy forest would have further reduced habitat suitability for *D. viverrinus*, and possibly a reduction in prey species such as invertebrates, small mammals and reptiles (Blackhall, 1980; Godsell, 1983) that today are typically associated with open grasslands and more arid environments. Modern-day species distributions indicate that *D. viverrinus* is predominantly associated with open grasslands, dry sclerophyll forests and woodlands in the drier east of Tasmania (Jones & Rose, 1996; Fancourt *et al.*, 2015), although they are still observed infrequently in sub-optimal habitat in low densities. As several *D. viverrinus* can utilise the same small, overlapping home range (Godsell, 1983), it is possible that the species could have persisted in pockets of more open habitat within the broader matrix of sub-optimal vegetation, with suitable refuges gradually disappearing with reduced fire management following the disappearance of humans from the island (Hope *et al.*, 1977). Since European settlement, extensive land clearing for agriculture and settlement has opened up around half of the island's vegetation, potentially providing more suitable habitat for open grassland species such as *D. viverrinus*. Indeed, some open grassland and woodland bird species have recolonised the island in recent decades, after dying out during the early Holocene (Ford & Paton, 1975; Hope *et al.*, 1977). However, while the current habitat may now be more compatible with *D. viverrinus* persistence, the climatic conditions remain sub-optimal (Fancourt *et al.*, 2015), suggesting the species would be unlikely to thrive on the island. Additionally, as *D. viverrinus* is predominantly insectivorous (Blackhall, 1980; Godsell, 1983), it's functional value as a predator of overabundant medium sized mammals would be limited, that role being more suited to a larger predator.

While modern-day *S. harrisii* is more commonly associated with open grasslands in agricultural areas of Tasmania, it has been found in all major vegetation types (Rounsevell *et al.*, 1991), suggesting the species could have persisted in the thicker forested vegetation of Kangaroo Island during the Holocene. However, recent climate modelling (Hunter *et al.*, 2015) suggests that *S. harrisii* is a cool-adapted species, with Kangaroo Island now being climatically unsuitable for its persistence (Fig. 1(a) in Hunter *et al.*, 2015). Furthermore, as the open grasslands were gradually succeeded by thicker vegetation, the loss of large herbivorous grazers with the changing environment (Hope *et al.*, 1977) would likely have depleted a formerly abundant prey base for *S. harrisii* which is known to consume predominantly large and medium sized herbivores (Jones & Barmuta, 1998). Accordingly, the combination of reduced prey availability and a warming climate may have contributed to the extirpation of *S. harrisii* on Kangaroo Island. As noted for *D. viverrinus*, recent changes to the island following European settlement have created more open, fragmented habitat that would likely benefit both *S. harrisii* and many medium and large-sized herbivores that form the bulk of its diet. However, while species such as brushtail possums (*T. vulpecula*) and tammar wallabies (*M. eugenii*) are now abundant on the island, *S. harrisii* is a specialised scavenger (Jones & Barmuta, 1998) and would likely scavenge on the abundance of carcasses from roadkill, culling and natural attrition in lieu of depredating live prey (Fancourt & Mooney, 2016). Furthermore, current climatic conditions on Kangaroo Island remain unsuitable for *S. harrisii* (Fig. 1(a) in Hunter *et al.*, 2015), suggesting that *S. harrisii* would not be an appropriate candidate for reintroduction to the island.

The modern-day distribution of *D. maculatus* on mainland Australia is most strongly associated with high annual mean rainfall (> 600 mm), high elevation, and extensive tracts of continuous forest (Burnett, 2001; Catling *et al.*, 2002). However, Troy (2014) found that *D. maculatus* distribution in Tasmania was best explained by warm temperature which is correlated with low elevation. Furthermore, while mainland *D. maculatus* is largely restricted to forested areas, Troy (2014) found that landscapes with low forest cover can still provide suitable habitat for *D. maculatus* in Tasmania. Troy (2014) hypothesised that the realised niches of mainland and Tasmanian *D. maculatus* differ due to differences in the composition of their predator guilds, with the apparent habitat preferences of the mainland *D. maculatus* possibly shaped top-down by intense competition from the introduced red fox, which is functionally absent from Tasmania (Invasive Species Branch, 2013). Accordingly, the predicted habitat associations of *D. maculatus* on the fox-free Kangaroo Island would more closely approximate those observed in Tasmania than on the mainland. In Tasmania, *D. maculatus* prefers forest and avoids pasture for home range placement, with home range size increasing with increasing habitat loss and fragmentation (Troy, 2014). This suggests that the reduction in open habitat and increasing forested habitat on Kangaroo Island (and King and Flinders Islands) during the Holocene would have supported smaller home ranges of *D. maculatus*, facilitating higher densities and increasing the likelihood of persistence. Additionally, *D. maculatus* is more arboreal and makes greater use of habitats with a structurally complex understory than both *S. harrisii* and *D. viverrinus* (Jones & Barmuta, 2000), possibly facilitating the prolonged persistence of *D. maculatus* on Kangaroo Island throughout the Holocene.

The recent extirpation of *D. maculatus* from Kangaroo, King and Flinders Islands appears likely to have been driven by a combination of anthropogenic factors including hunting and persecution by European settlers and dogs and habitat clearing (see Appendix S4). Similar to the extensive clearance of vegetation across much of mainland Australia (Bradshaw, 2012), large areas of vegetation on Kangaroo Island were extensively burned and cleared for development and conversion to pasture, however this wasn't substantial until the implementation of post WWII soldier settler schemes and application of the cure for coast disease (Interdepartmental Committee on Vegetation Clearance, 1976). Similar broad scale habitat clearance occurred on King Island commencing in the late 1800s, and later on Flinders Island (see Appendix S5), resulting in the more extensive open habitats observed today. As noted previously, while *D. maculatus* can utilise habitat with low forest cover, home ranges would need to be larger in more open habitats (Troy, 2014). As female *D. maculatus* occupy exclusive territories (Glen & Dickman, 2006a), the carrying capacity of the more open habitat would be much lower than in remnant tracts of native forest, rendering the species more vulnerable to other threatening processes. Persecution of *Dasyurus* spp. has been recorded from Kangaroo Island (Leigh, 1839) as well as both King and Flinders Islands (see Appendix S5), primarily for killing domestic poultry, but occasionally for its attractive spotted pelage. This persecution accords with numerous accounts across mainland Australia, commencing at the time of European settlement in 1788 through to the mid-1900s (Peacock & Abbott, 2013). While wild dogs were not reported as present on Kangaroo Island, they were known to occur on Flinders and King Islands, possibly left there by the sealers, and potentially depredating *D. maculatus* on those islands. While the role of these drivers in the extirpation are necessarily speculative, the weight of evidence suggests that a combination of preventable, anthropogenic factors contributed to the local demise of *D. maculatus* on all three islands. As the species is now legally protected, the suitable habitat and climatic conditions on Kangaroo Island suggest that *D. maculatus* would be the most appropriate candidate marsupial carnivore for reintroduction to the island.

The ecological function performed by *D. maculatus* would likely be broader than that of *D. viverrinus*, *D. geoffroii* and *S. harrisii*, and more appropriate for the management of the Kangaroo Island's unique faunal assemblage. Evidence from Tasmania indicates that *D. maculatus* exhibits a high degree of dietary overlap with *D. viverrinus* and *S. harrisii* (Jones & Barmuta, 1998), suggesting a broader dietary niche than the other two species. Additionally, as the activity of *D. maculatus* is more arboreal than either *D. viverrinus*, *D. geoffroii* or *S. harrisii* (Jones & Barmuta, 2000), its prey base is not restricted to ground-dwelling species. Dietary studies from mainland Australia and Tasmania indicate that *D. maculatus* is a generalist predator of both arboreal and ground-dwelling species, with diet dominated by medium-sized mammals abundant in the landscape, including brushtail possums (*Trichosurus* spp.), rabbits (*O. cuniculus*), pademelons (*Thylogale* spp.) and wallabies (*Macropus* spp.), although small and large mammals and birds are also consumed (Belcher, 1995; Jones & Barmuta, 1998; Glen & Dickman, 2006b; Dawson *et al.*, 2007). This suggests that *D. maculatus* might assist through predation of overabundant common brushtail possums (*T. vulpecula*) and tammar wallabies (*M. eugenii*) on Kangaroo Island, although its ability to substantially reduce population abundance of these species is unknown. As the feral cat population on Kangaroo Island is targeted for eradication by 2030 through the Kangaroo Island Feral Cat Eradication Project (Natural Resources Kangaroo Island, 2015), *D. maculatus* would be the most appropriate native predator to fill this vacant niche due to its similar size and diet (Glen *et al.*, 2011). However, the lower fecundity of *D. maculatus* (*cf*. feral cats) and the territoriality of females (Glen & Dickman, 2006a) suggests that populations would be unlikely to attain overabundance and hence would require minimal management intervention to control population size. Furthermore, as a native predator, *D. maculatus* may also confer a conservation advantage to threatened native prey species that have, until recently, evolved in the presence of *D. maculatus*, and would therefore be more vulnerable to predation by introduced feral cats to which they have not evolved appropriate anti-predator responses (Paolucci *et al.*, 2013).

Presently, two subspecies of *D. maculatus* are recognised: *D. maculatus gracilis* is restricted to the Wet Tropics region of Northern Queensland, while *D. maculatus maculatus* occurs throughout NSW, Victoria and Tasmania (Belcher *et al.*, 2008). The demarcation of these subspecies was originally based on morphological differences, with *D. m. gracilis* being much smaller than its southern counterparts. However, genetic differences indicate that the demarcation should occur between the Tasmanian population and the Australian mainland populations, as the mainland populations of *D. m. maculatus* and *D. m. gracilis* are more closely related than the mainland and Tasmanian populations of *D. m. maculatus* (Firestone *et al.*, 1999). While the genetic origins of the Kangaroo Island *D. maculatus* are unknown, we suggest that the contemporary dentary specimen dated by (Walshe, 2014) be tested to determine its genetic relatedness to extant populations of *D. maculatus*, thereby informing future reintroductions as to the most appropriate source population for founders.

When considering species for reintroduction, modern-day faunal assemblages will rarely be indicative of the species assemblages that persisted at the time of European colonisation. Land clearing and required coexistence with humans and their various enterprises (agriculture, tourism, development) may have rendered modern ecosystems unsuitable for species that were well suited only 200 years prior, whilst inadvertently creating more favourable habitat for other species. Accordingly, it is important to collate and review not only contemporary accounts of species occurrence, but also historic and prehistoric evidence to assist in reconstructing changes in faunal assemblages over time, and to understand the likely reasons for those changes so that species reintroductions can be more fully informed. While such information is often scant and typically found outside of the traditional scientific literature (e.g. newspapers, journals, ship logs of early explorers, museum specimens and fossils), this study highlights the usefulness of these non-traditional information sources in understanding which species were present and when, although their value in inferring species absence or extirpation is inherently limited. For example, in many cases, the youngest fossil is unlikely to reflect the true timing of each species' extirpation, but rather the timing of conditions suitable for fossilisation, with the final date of extirpation potentially occurring hundreds or thousands of years later. Similarly, the failure to observe a species in recent times does not demonstrate that the species is actually absent, but merely that it was not detected. Whilst we acknowledge the limitations of such evidence (or the absence of evidence), we consider that incorporating this non-traditional evidence is a vital part of understanding historic and prehistoric faunal assemblages to inform reintroductions, providing new insights that cannot be elucidated from contemporary species' occurrence and distributions alone.

Conclusion

Our findings suggest that *D. maculatus* would be the most suitable marsupial predator to reintroduce to Kangaroo Island, assisting to restore vital ecological function whilst contributing to the conservation of the species. Modern-day habitat and climatic conditions on Kangaroo Island are consistent with *D. maculatus* persistence, suggesting that the species would likely thrive on the island. While the current open habitat would likely be suitable for *D. viverrinus* or *D. geoffroii*, these species' ability to fill the required ecological function of a predator of medium-sized mammals would be questionable. In contrast, available evidence suggests that the current-day bioclimatic envelope would render Kangaroo Island unsuitable for *S. harrisii*, and hence reintroduction of this species should be considered with caution. Given the similarities in species persistence and drivers of extirpation across Kangaroo, King and Flinders Islands, reintroductions of *D. maculatus* to King Island and/or Flinders Island should also be considered to assist in restoring critical ecological function on those islands, whilst helping to conserve a threatened marsupial carnivore.

Acknowledgements

We thank Belinda Bauer (Tasmanian Museum and Art Gallery), Wayne Gerdtz and Bentley Bird (Museum Victoria), Tammy Gordan (Queen Victoria Museum and Art Gallery) and Heather Janetzki (Queensland Museum) for assisting with sourcing and identification of museum samples. Kangaroo Island Natural Resources Management are thanked for provision of the 1976 report 'Interdepartmental Committee on Vegetation Clearance' and Brendan Lay (retired) is thanked for confirming Figure 2.4 was accurate having been derived from aerial photographs.

References

Adams, S.J., McDowell, M.C. & Prideaux, G.J. (2016) Understanding accumulation bias in the ecological interpretation of archaeological and paleontological sites on Kangaroo Island, South Australia. *Journal of Archaeological Science: Reports*, **7**, 715-729.

Alleway, H.K. & Connell, S.D. (2015) Loss of an ecological baseline through the eradication of oyster reefs from coastal ecosystems and human memory. *Conservation Biology*, **29**, 795-804.

Ball, D. & Carruthers, S. (1999) Vegetation Mapping. *A Biological Survey of Kangaroo Island, South Australia, 1989 & 1990* (ed. by A.C. Robinson and D.M. Armstrong), pp. 159-185. Heritage and Biodiversity Section, Department for Environment, Heritage and Aboriginal Affairs, Adelaide, South Australia.

Belcher, C. (1995) Diet of the tiger quoll (Dasyurus maculatus). *Wildlife Research*, **22**, 341-357.

Belcher, C., Burnett, S. & Jones, M.E. (2008) Spotted-tailed Quoll: *Dasyurus maculatus*. *The Mammals of Australia* (ed. by S.M. Van Dyck and R. Strahan), pp. 60-62. Reed New Holland, Sydney.

Belperio, A.P. & Flint, R.B. (1999) Geomorphology and Geology. *A Biological Survey of Kangaroo Island, South Australia, 1989 & 1990* (ed. by A.C. Robinson and D.M. Armstrong), pp. 19-31. Heritage and Biodiversity Section, Department for Environment, Heritage and Aboriginal Affairs, Adelaide, South Australia.

Berger, L., Speare, R., Daszak, P., Green, D.E., Cunningham, A.A., Goggin, C.L., Slocombe, R., Ragan, M.A., Hyatt, A.D., McDonald, K.R., Hines, H.B., Lips, K.R., Marantelli, G. & Parkes, H. (1998) Chytridiomycosis causes amphibian mortality associated with population declines in the rain forests of Australia and Central America. *Proceedings of the National Academy of Sciences*, **95**, 9031-9036.

Bertness, M.D., Brisson, C.P., Coverdale, T.C., Bevil, M.C., Crotty, S.M. & Suglia, E.R. (2014) Experimental predator removal causes rapid salt marsh die-off. *Ecology Letters*, **17**, 830-835.

Blackhall, S. (1980) Diet of the eastern native-cat, *Dasyurus viverrinus* (Shaw), in southern Tasmania. *Australian Wildlife Research*, **7**, 191-198.

Blehert, D.S., Hicks, A.C., Behr, M., Meteyer, C.U., Berlowski-Zier, B.M., Buckles, E.L., Coleman, J.T.H., Darling, S.R., Gargas, A., Niver, R., Okoniewski, J.C., Rudd, R.J. & Stone, W.B. (2009) Bat White-Nose Syndrome: An Emerging Fungal Pathogen? *Science*, **323**, 227-227.

Bradshaw, C.J.A. (2012) Little left to lose: deforestation and forest degredation in Australia since European colonisation. *Journal of Plant Ecology*, **5**, 109-120.

Brook, B.W., Sodhi, N.S. & Bradshaw, C.J.A. (2008) Synergies among extinction drivers under global change. *Trends in Ecology & Evolution*, **23**, 453-460.

Burbidge, A.A. (1999) Conservation values and management of Australian islands for non-volant mammal conservation. *Australian Mammalogy*, **21**, 67-74.

Burbidge, A.A. & McKenzie, N.L. (1989) Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. *Biological Conservation*, **50**, 143-198.

Burnett, S. (2001) *Ecology and conservation status of the northern spot-tailed quoll Dasyurus maculatus with reference to the future of Australia's marsupial carnivores*. PhD, James Cook University of North Queensland, Townsville.

Catling, P.C., Burt, R.J. & Forrester, R.I. (2002) Models of the distribution and abundance of ground-dwelling mammals in the eucalypt forests of north-eastern New South Wales in relation to environmental variables. *Wildlife Research*, **29**, 313-322.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M. & Palmer, T.M. (2015) Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Science Advances*, **1**, e1400253.

Clark, R. & Lampert, R. (1981) Past changes in burning regime as markers of man's activity on Kangaroo Island, South Australia. *Terra Australis*, **5**, 1-86.

Creel, S. & Christianson, D. (2008) Relationships between direct predation and risk effects. *Trends in Ecology & Evolution*, **23**, 194-201.

Crooks, K.R. & Soulé, M.E. (1999) Mesopredator release and avifaunal extinctions in a fragmented system. *Nature*, **400**, 563-566.

Dawson, J.P., Claridge, A.W., Triggs, B. & Paull, D.J. (2007) Diet of a native carnivore, the spotted-tailed quoll (Dasyurus maculatus), before and after an intense wildfire. *Wildlife Research*, **34**, 342-351.

Draper, N. (1999) Land-Use History: The History of Aboriginal Land Use on Kangaroo Island. *A Biological Survey of Kangaroo Island, South Australia, 1989 & 1990* (ed. by A.C. Robinson and D.M. Armstrong), pp. 33-48. Heritage and Biodiversity Section, Department for Environment, Heritage and Aboriginal Affairs, Adelaide, South Australia.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R. & Wardle, D.A. (2011) Trophic downgrading of planet earth. *Science*, **333**, 301-306.

Fancourt, B.A. & Mooney, N. (2016) Tasmanian devils are likely a blunt instrument: A comment on Hunter et al. (2015). *Biological Conservation*, DOI: 10.1016/j.biocon.2016.01.022

Fancourt, B.A., Nicol, S.C. & Hawkins, C.E. (2013) Evidence of rapid population decline of the eastern quoll (*Dasyurus viverrinus*) in Tasmania. *Australian Mammalogy*, **35**, 195-205.

Fancourt, B.A., Bateman, B.L., VanDerWal, J., Nicol, S.C., Hawkins, C.E., Jones, M.E. & Johnson, C.N. (2015) Testing the role of climate change in species decline: is the eastern quoll a victim of a change in the weather? *PLoS ONE*, **10**, e0129420.

Firestone, K.B., Elphinstone, M.S., Sherwin, W.B. & Houlden, B.A. (1999) Phylogeographical population structure of tiger quolls Dasyurus maculatus (Dasyuridae: Marsupialia), an endangered carnivorous marsupial. *Molecular Ecology*, **8**, 1613-1625.

Forbes, M.S., Kohn, M.J., Bestland, E.A. & Wells, R.T. (2010) Late Pleistocene environmental change interpreted from δ13C and δ18O of tooth enamel from the Black Creek Swamp Megafauna site, Kangaroo Island, South Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **291**, 319-327.

Ford, H. & Paton, D. (1975) Impoverishment of the avifauna of Kangaroo Island. *Emu*, **75**, 155-156.

Glen, A.S. & Dickman, C.R. (2006a) Home range, denning behaviour and microhabitat use of the carnivorous marsupial Dasyurus maculatus in eastern Australia. *Journal of Zoology*, **268**, 347-354.

Glen, A.S. & Dickman, C.R. (2006b) Diet of the spotted-tailed quoll (Dasyurus maculatus) in eastern Australia: Effects of season, sex and size. *Journal of Zoology*, **269**, 241-248.

Glen, A.S., Pennay, M., Dickman, C.R., Wintle, B.A. & Firestone, K.B. (2011) Diets of sympatric native and introduced carnivores in the Barrington Tops, eastern Australia. *Austral Ecology*, **36**, 290-296.

Godsell, J. (1983) *Ecology of the Eastern Quoll, Dasyurus viverrinus (Dasyuridae: Marsupialia)*. PhD, Australian National University, Canberra.

Guiler, E.R. (1985) *Thylacine: The Tragedy of the Tasmanian Tiger*. Oxford University Press, Melbourne.

Hawkins, C.E., Baars, C., Hesterman, H., Hocking, G.J., Jones, M.E., Lazenby, B., Mann, D., Mooney, N., Pemberton, D., Pyecroft, S., Restani, M. & Wiersma, J. (2006) Emerging disease and population decline of an island endemic, the Tasmanian devil *Sarcophilus harrisii*. *Biological Conservation*, **131**, 307-324.

Hoffmann, M., Belant, J.L., Chanson, J.S., Cox, N.A., Lamoreux, J., Rodrigues, A.S.L., Schipper, J. & Stuart, S.N. (2011) The changing fates of the world's mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **366**, 2598-2610.

Hope, J.H. (1973) Mammals of the Bass Strait islands. *Proceedings of the Royal Society of Victoria*, **85**, 163-195.

Hope, J.H. (1974) Biogeography and Ecology in Tasmania XIV. The biogeography of the mammals of the islands of Bass Strait. *Monographiae Biologicae* (ed. by W.D. Williams), pp. 397-415. Springer, Netherlands.

Hope, J.H., Lampert, R.J., Edmondson, E., Smith, M.J. & Tets, G.F.v. (1977) Late Pleistocene Faunal Remains from Seton Rock Shelter, Kangaroo Island, South Australia. *Journal of Biogeography*, **4**, 363-385.

Hunter, D.O., Britz, T., Jones, M. & Letnic, M. (2015) Reintroduction of Tasmanian devils to mainland Australia can restore top-down control in ecosystems where dingoes have been extirpated. *Biological Conservation*, **191**, 428-435.

Interdepartmental Committee on Vegetation Clearance (1976) Vegetation Clearance in South Australia. In. Department for the Environment, Adelaide, SA.

Invasive Species Branch (2013) Fox Eradication Program Review Recommendations. In, Prospect, Tasmania.

Jennings, J.N. (1971) Sea Level Changes and Land Links. *Aboriginal Man and Environment in Australia* (ed. by D.J. Mulvaney and J. Golson), pp. 1-13. Australian National University Press, Canberra.

Jones, M.E. & Rose, R.K. (1996) Preliminary assessment of distribution and habitat associations of the spotted-tailed quoll (*Dasyurus maculatus maculatus*) and eastern quoll (*D. viverrinus*) in Tasmania to determine conservation and reservation status. In. Report to the Tasmanian Regional Forest Agreement Environment and Heritage Technical Committee, Tasmanian Public Land Use Commission, Hobart, Tasmania.

Jones, M.E. & Barmuta, L.A. (1998) Diet overlap and relative abundance of sympatric dasyurid carnivores: a hypothesis of competition. *Journal of Animal Ecology*, **67**, 410-421.

Jones, M.E. & Barmuta, L.A. (2000) Niche differentiation among sympatric Australian dasyurid carnivores. *Journal of Mammalogy*, **81**, 434-447.

Jones, R. (1977) Man as an element of a continental fauna: the case of the sundering of the Bassian bridge. *Sunda and Sahul; prehistoric studies in Southeast Asia, Melanesia and Australia* (ed. by F.J. Allen, J. Golson and R. Jones), pp. 317-386. Academic Press, New York.

Lambeck, K. & Chappell, J. (2001) Sea level change through the last glacial cycle. *Science* **292**, 679-686.

Langeluddecke, C. (2001) *The small faunal taphonomy and zooarchaeology of Cape du Couedic Rockshelter, Kangaroo Island, South Australia*. Flinders University, Adelaide.

Lavery, T.H., Fisher, D.O., Flannery, T.F. & Leung, L.K.P. (2013) Higher extinction rates of dasyurids on Australo-Papuan continental shelf islands and the zoogeography of New Guinea mammals. *Journal of Biogeography*, **40**, 747-758.

Leigh, W.H. (1839) *Reconnoitering Voyages and Travels, with Adventures in the new colonies of South Australia; a particular description of the Town of Adelaide, and Kangaroo Island; and an account of the Present State of Sydney and Parts Adjacent, including visits to the Nicobar and other islands of the Indian Seas, Calcutta, the Cape of Good Hope, and St. Helena, During the Years 1836, 1837, 1838*. Smith, Elder and Co. Cornhill, London.

Lesueur, C.A. & Petit, N.M. (1807) *Atlas Historique, Part I*. Imprimerie Impériale, Paris.

Marshall, L. & Hope, J. (1973) A reevaluation of *Dasyurus bowlingi* Spencer and Kershaw 1910 (Marsupialia, Dasyuridae) from King Island, Bass Strait. *Proceedings of the Royal Society of Victoria*, **85**, 225-236.

McCallum, H., Jones, M., Hawkins, C., Hamede, R., Lachish, S., Sinn, D.L., Beeton, N. & Lazenby, B. (2009) Transmission dynamics of Tasmanian devil facial tumor disease may lead to disease-induced extinction. *Ecology*, **90**, 3379-92.

McDowell, M.C. (2013) *Late Quaternary faunal responses to environmental change and isolation on a large Australian land-bridge island*. Flinders University, Adelaide.

McDowell, M.C. (2014) Holocene vertebrate fossils aid the management and restoration of Australian ecosystems. *Ecological Management & Restoration*, **15**, 58-63.

McDowell, M.C., Prideaux, G.J., Walshe, K., Bertuch, F. & Jacobsen, G.E. (2015) Re-evaluating the Late Quaternary fossil mammal assemblage of Seton Rockshelter, Kangaroo Island, South Australia, including the evidence for late-surviving megafauna. *Journal of Quaternary Science*, **30**, 355-364.

Morris, K., Page, M., Kay, R., Renwick, J., Desmond, A., Comer, S., Burbidge, A., Kuchling, G. & Sims, C. (2015) Forty years of fauna translocations in Western Australia: Lessons learned. *Advances in Reintroduction Biology of Australian and New Zealand Fauna* (ed. by D. Armstrong, M. Hayward, D. Moro and P. Seddon), pp. 217-235. CSIRO Publishing, Clayton South Vic.

Natural Resources Kangaroo Island (2015) Feral cat eradication on Kangaroo Island 2015-2030 prospectus. Draft for consultation. In, Unpublished.

Palomares, F. & Caro, T.M. (1999) Interspecific killing among mammalian carnivores. *The American Naturalist*, **153**, 492-508.

Paolucci, E.M., MacIsaac, H.J. & Ricciardi, A. (2013) Origin matters: alien consumers inflict greater damage on prey populations than do native consumers. *Diversity and Distributions*, **19**, 988-995.

Peacock, D. & Abbott, I. (2013) The role of quoll (*Dasyurus*) predation in the outcome of pre-1900 introductions of rabbits (*Oryctolagus cuniculus*) to the mainland and islands of Australia. *Australian Journal of Zoology*, **61**, 206-280.

Peacock, D. & Abbott, I. (2014) When the “native cat” would “plague”: historical hyper-abundance in the quoll (Marsupialia: Dasyuridae) and an assessment of the role of disease, cats and foxes in its curtailment. *Australian Journal of Zoology*, **62**, 294-344.

Péron, F. & de Freycinet, L. (1816) *Voyage de découvertes aux Terres Australes, exécuté sur les corvettes le Géographe, le Naturaliste, et la goëlette le Casuarine, pendant les années 1800, 1801, 1802, 1803 et 1804. Historique: Tome Second*, Paris.

Pimm, S., Raven, P., Peterson, A., Şekercioğlu, Ç.H. & Ehrlich, P.R. (2006) Human impacts on the rates of recent, present, and future bird extinctions. *Proceedings of the National Academy of Sciences*, **103**, 10941-10946.

Plomley, N.J.B. (1966) *Friendly Mission : The Tasmanian Journals and Papers of George Augustus Robinson 1829-1834*. Hobart, Tasmanian Historical Research Association.

Plomley, N.J.B. (1987) *Weep In Silence. A History of the Flinders Island Aboriginal Settlement with the Flinders Island Journal of George Augustus Robinson 1835-1839*. Blubber Head Press, Hobart.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D. & Wirsing, A.J. (2014) Status and ecological effects of the world's largest carnivores. *Science*, **343**

Robinson, A.C. (1999) European History. *A Biological Survey of Kangaroo Island, South Australia, 1989 & 1990* (ed. by A.C. Robinson and D.M. Armstrong), pp. 49-56. Heritage and Biodiversity Section, Department for Environment, Heritage and Aboriginal Affairs, Adelaide, South Australia.

Robinson, A.C. & Kemper, C.M. (1999) Mammals. *A Biological Survey of Kangaroo Island, South Australia, 1989 & 1990* (ed. by A.C. Robinson and D.M. Armstrong), pp. 186-203. Heritage and Biodiversity Section, Department for Environment, Heritage and Aboriginal Affairs, Adelaide, South Australia.

Robinson, A.C. & Armstrong, D.M. (ed.^eds) (1999) *A Biological Survey of Kangaroo Island, South Australia, 1989 & 1990*. Heritage and Biodiversity Section, Department for Environment, Heritage and Aboriginal Affairs, Adelaide, South Australia.

Rounsevell, D.E., Taylor, R.J. & Hocking, G.J. (1991) Distribution records of native terrestrial mammals in Tasmania. *Wildlife Research*, **18**, 699-717.

Saltre, F., Rodriguez-Rey, M., Brook, B.W., Johnson, C.N., Turney, C.S.M., Alroy, J., Cooper, A., Beeton, N., Bird, M.I., Fordham, D.A., Gillespie, R., Herrando-Perez, S., Jacobs, Z., Miller, G.H., Nogues-Bravo, D., Prideaux, G.J., Roberts, R.G. & Bradshaw, C.J.A. (2016) Climate change not to blame for late Quaternary megafauna extinctions in Australia. *Nature Communications*, **7**

Schwerdtfeger, P. (2002) Climate. *Natural History of Kangaroo Island* (ed. by M. Davies, C.R. Twidale and M.J. Taylor), pp. 47-53. Royal Society of South Australia, Adelaide.

Singh, G., Kershaw, A.P. & Clark, R. (1981) Quaternary vegetation and fire history in Australia. *Fire and the Australian Biota* (ed. by A.M. Gill, R.H. Groves and I.R. Noble), pp. 23-54. Australian Academy of Science, Canberra.

Spencer, B. & Kershaw, J.A. (1910) A Collection of Sub-fossil Bird and Marsupial Remains from King Island, Bass Strait. *Memoirs of the National Museum, Mellbourne*, **3**, 5-36.

Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L. & Waller, R.W. (2004) Status and Trends of Amphibian Declines and Extinctions Worldwide. *Science*, **306**, 1783-1786.

Suraci, J.P., Clinchy, M., Dill, L.M., Roberts, D. & Zanette, L.Y. (2016) Fear of large carnivores causes a trophic cascade. *Nature Communications*, **7**, doi 10.1038/ncomms10698.

Taylor, R. (2002) *Unearthed: The Aboriginal Tasmanians of Kangaroo Island*. Wakefield Press, Kent Town.

Threatened Species Section (2012) *King Island Biodiversity Management Plan*. Department of Primary Industries, Parks, Water and Environment, Hobart.

Troy, S.N. (2014) *Spatial ecology of the Tasmanian spotted-tailed quoll*. PhD thesis, University of Tasmania, Hobart.

Waite, E.R. & Wood Jones, F. (1927) The fauna of Kangaroo Island, South Australia. No. 2. The mammals. *Transactions of the Royal Society of South Australia*, **51**, 322-325.

Walker, B. (1995) Conserving Biological Diversity through Ecosystem Resilience. *Conservation Biology*, **9**, 747-752.

Walshe, K. (2014) Archaeological evidence for a sealer's and wallaby hunter's skinning site on Kangaroo Island, South Australia. *The Journal of Island and Coastal Archaeology,*, **9**, 130-143.

Woinarski, J.C.Z., Burbidge, A.A. & Harrison, P.L. (2014) *Action Plan for Australian Mammals 2012*. CSIRO Publishing, Melbourne.

Woinarski, J.C.Z., Burbidge, A.A. & Harrison, P.L. (2015) Ongoing unraveling of a continental fauna: Decline and extinction of Australian mammals since European settlement. *Proceedings of the National Academy of Sciences,* Woinarski, J.C.Z., Legge, S., Fitzsimons, J.A., Traill, B.J., Burbidge, A.A., Fisher, A., Firth, R.S.C., Gordon, I.J., Griffiths, A.D., Johnson, C.N., McKenzie, N.L., Palmer, C., Radford, I., Rankmore, B., Ritchie, E.G., Ward, S. & Ziembicki, M. (2011) The disappearing mammal fauna of northern Australia: context, cause, and response. *Conservation Letters*, **4**, 192-201.

Woodroffe, R., Thirgood, S. & Rabinowitz, A. (2005) The future of coexistence: resolving human-wildlife conflicts in a changing world. *People and Wildlife, Conflict or Co-existence?* (ed. by R. Woodroffe, S. Thirgood and A. Rabinowitz), pp. 388-405. Cambridge University Press, Cambridge, United Kingdom.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Table listing evidence, specimens and accounts to inform the persistence of marsupial carnivores on Kangaroo Island

Appendix S2 Table listing evidence, specimens and accounts to inform the persistence of marsupial carnivores on King Island

Appendix S3 Table listing evidence, specimens and accounts to inform the persistence of marsupial carnivores on Flinders Island

Appendix S4 Table listing evidence, accounts, insights and events to inform the timing and likely factors contributing to the extirpation of marsupial carnivores on Kangaroo Island

Appendix S5 Table listing evidence, accounts, insights and events to inform the timing and likely factors contributing to the extirpation of marsupial carnivores on King and Flinders Islands

BIOSKETCH

David E. Peacock is a research officer with Biosecurity South Australia with a research interest in historical ecology to guide ecological restoration. He and his colleagues have a research interest in establishing baseline knowledge of the historical and modern distributions and survival histories of Australia's threatened fauna, primarily with a goal of enabling and guiding restorative management practices, such as translocations.

Author contributions: IA reviewed Leigh (1839) and sourced the 1837 post-European account of *Dasyurus maculatus* on Kangaroo Island, which stimulated this study; DEP, BAF, MCM and IA collected the data; DEP, BAF and MCM wrote the manuscript; IA edited the manuscript; MCM provided subfossil data and prepared the figures.

Table 1. Summary of evidence and accounts of marsupial carnivores on Kangaroo Island (South Australia), King Island and Flinders Island (Tasmania).

Closed circles indicate evidence (fossil, skull, skin, bone specimen), open circles indicate observation/anecdote/report, dash indicates no records. Individual specimens and accounts are listed in Appendices S1-S3.

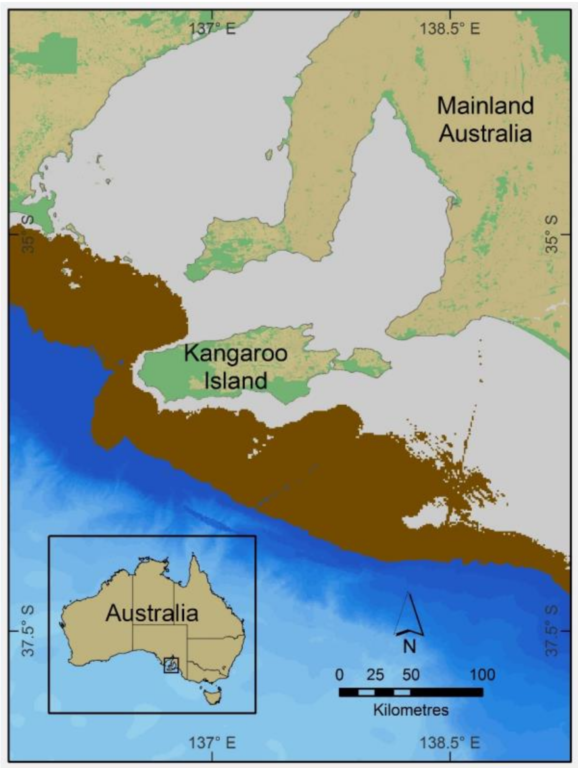
Evidence	Species	Kangaroo Island	King Island	Flinders Island
Contemporary evidence	*D. viverrinus*	○	○	○
	D. geoffroii	●	-	-
	D. maculatus	● ○	● ○	○
	S. harrisii	-	-	-
	T. cynocephalus	-	-	-

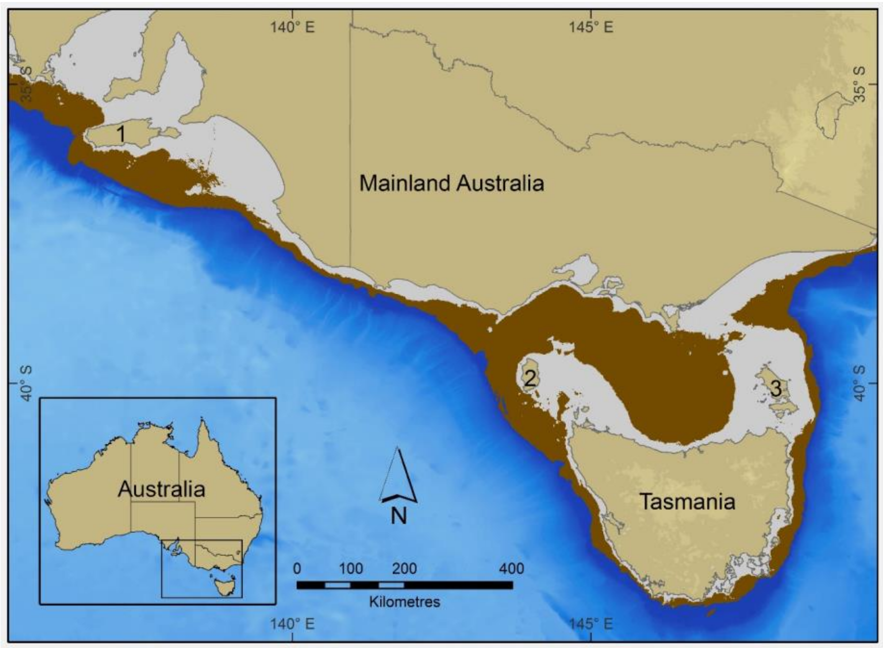
Fossil evidence	*D. viverrinus*	●	-	●
	D. geoffroii	●	-	-
	D. maculatus	●	●	●
	S. harrisii	●	-	●
	T. cynocephalus	●	-	-

Figure 1. Map of Kangaroo Island showing its proximity to the Australian mainland and its remnant native vegetation cover. Tan shading represents the present-day exposed land mass and green shading indicates current remnant native vegetation. Inset shows location of study area within southern Australia.

Figure 2. Location of Kangaroo Island (1) in relation to King Island (2) and Flinders Island (3) and their historic connectivity to the Australian mainland. Grey shading represents the exposed area of the continental land bridge at 14 kya (60 m below present sea level (PSL)); brown shading represents the exposed area during the height of the last glacial maximum 22-17 kya (125 m below PSL); tan shading represents the present-day exposed land mass (SOURCE REF: Geosciences Australia accessed February 2017). Inset shows location of study area within south-eastern Australia.

Commented [2]: Do we need this?


137° E
138.5° E
Mainland
Australia
Kangaroo
Island
35° S
35° S
Australia
37.5° S
37.5° S
N
0 25 50 100
Kilometres
137° E
138.5° E


140° E
145° E
35° S
40° S
Mainland Australia
1
2
3
Tasmania
Australia
N
0
100
200
400
Kilometres